PATTERNS OF ABUNDANCE AND HABITAT USE BY *NANNOPERCA OBSCURA* (YARRA PYGMY PERCH) AND *NANNOPERCA AUSTRALIS* (SOUTHERN PYGMY PERCH)

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Nannoperca obscura (Yarra pygmy perch) and *Nannoperca australis* (Southern pygmy perch) appear to have undergone differential declines in abundance and distribution since European settlement. We examined patterns of abundance and habitat use of these species in allopatry and sympatry. While the pattern of habitat use by *N. obscura* was very similar to that of *N. australis* in allopatry, it was restricted to only a small proportion of available habitats and excluded from the floodplain when sympatric with *N. australis*. Habitats utilised by *N. obscura* when sympatric with *N. australis* were also occupied by relatively large numbers of *Perca fluviatilis* (Redfin). We speculate that the different patterns in abundance of pygmy perch among sites were largely due to interactions between size-fecundity relationships, habitat use sometimes mediated by interspecific competition, and predation intensity by *P. fluviatilis*.

Key words:Nannoperca obscura, N. australis

NANNOPERCA AUSTRALIS (Southern pygmy perch) and *Nannoperca obscura* (Yarra pygmy perch) are small, perch-like fishes endemic to south-eastern Australia. The two species are morphologically (Kuiter and Allen 1986) and ecologically similar (Backhouse & Gooley, 1979; Kuiter et al. 1996). While *N. australis* can attain a maximum size of 85 mm, *N. obscura* is slightly smaller, reaching a maximum size of 75 mm (Allen et al. 2002). Both species inhabit slow flowing or still waters with abundant aquatic vegetation and are often found together (Kuiter et al. 1996). Their diets are similar and include planktonic crustaceans, aquatic insects and their larvae (Kuiter et al. 1996). The breeding season of *N. obscura* (September – October) overlaps with that of *N. australis* (September – January) (Allen et al. 2002).

Nannoperca obscura has been recorded from only 24 localities in southwestern Victoria and southeastern South Australia and appears to have undergone large-scale reductions in its distribution and abundance since European settlement (Kuiter et al. 1996; DNRE 1998). It has been suggested that the decline is probably due to habitat loss and modification, and interactions with introduced species (Wager & Jackson 1993; Kuiter et al. 1996). The species is considered 'threatened' and currently listed as 'vulnerable' (Wager & Jackson 1993; Groombridge & Mace 1994).

While *N. australis* is still considered a common and widespread species in Victoria (Koehn & O'Connor 1990), it also appears to have suffered population declines, although not as severe as *N. obscura* (Kuiter et al. 1996). Although habitat loss and modification have been identified as probable causes of their declines, no detailed studies have been carried out on habitat use of *N. obscura* and *N. australis*. This study compares habitat use of these two species of pygmy perch during spring-summer, and hypotheses are proposed to explain the differential decline of *N. obscura* and *N. australis*.

METHODS

Site Selection

Habitat use by sympatric *N. obscura* and *N. australis* was investigated at two sites in Deep Creek. Deep Creek is a second order stream located in south central Victoria that flows south into the Maribyrnong River system. The upper reaches of Deep Creek contain slow moving water most of the year, with a silt and gravel substratum. The Deep Creek 1 site was located at Linehan's Bridge (37°15'S 144°42'W), and the Deep Creek 2 site was located approximately 2 km downstream at Mustey's Bridge (37°15'S 144°44'W). Habitat use by *N. obscura* in the absence of *N. australis* was investigated at Woady Yaloak River, which represents the only known allopatric population of this species (DNRE 1998). The Woady Yaloak River is a third order stream located in southwest Victoria that runs into Lake Corangamite. It is normally slow flowing, with a mud, sand and gravel bottom. The Woady Yaloak River site was located at the Hamilton Highway bridge (37°47'S 143°34'W). Deep Creek sites were sampled on four occasions, and Woady Yaloak River on two occasions.

Site Descriptions

The physical characteristics of the three sites used in the study were very similar. They were approximately 40 m long and 10 m wide and consisted of a number of well-vegetated, shallow (< 1 m) pools and sparsely vegetated, deep (1 m - 1.5 m) pools. At Woady Yaloak River and Deep Creek 1 low lying inset benches (mini-floodplains) were inundated throughout the sampling period. This created shallow (400 mm depth), low flow habitats containing both semiaquatic and aquatic vegetation. The land surrounding the sites is primarily used for grazing, and little native vegetation remains.

Fish Abundances

Preliminary sampling was conducted at both Deep Creek sites in September 1998. Subsequent sampling occurred once a month between October 1998 and January 1999 except for Deep Creek 1, which was not sampled in January due to low water levels, and Woady Yaloak River, which was not sampled in October and November.

Fish abundances were determined using unbaited funnel traps (commonly referred to as bait traps). Traps measured 500 mm x 250 mm x 250 mm, with 50 mm (diameter) openings located at both ends and a mesh diameter of 4 mm. Abundances were standardised (number of fish caught per trap per hour) in order to account for variation in trapping effort.

Habitat Use

To determine habitat use by fish species, a trapping regime using stratified sampling was employed (Schaeffer et al. 1996; Sutherland 1996). Previous observations indicate that both *N. obscura* and *N. australis* are closely associated with aquatic macrophytes (Backhouse & Gooley 1979; Humphries 1995; Kuiter et al. 1996). Four structurally different habitat types were recognised at each site: submerged and emergent plants with very fine or feathery leaves; emergent plants with narrow leaves; mixture of both types of plants and; open water (channel). Six funnel traps were placed randomly within each habitat. At Woady Yaloak River and Deep Creek 1 an additional 6 traps were placed in floodplain habitats to determine floodplain use by pygmy perch. Traps were always placed more than 2 metres apart. Traps were set for a 24-hour period, and fish removed at dusk and dawn. At the end of the sampling period fish were released immediately after being measured (standard length (SL) to the nearest 1 mm) back into the habitat in which they had been caught. Very light pressure on the belly of females was applied to determine if they were 'spawning' (Kesteven 1960).

Data were analysed using the statistical package JMP (SAS Institute 1995). The Shapiro-Wilk test for normality was performed on all the data, and equality of variances was tested using the O'Brians 0.5 test (Sokal & Rohlf 1995). Parametric or non-parametric statistical tests were used in the analysis, depending upon the outcome of these tests. Abundance data were square root transformed prior to analysis, as some were not normally distributed. Because individual trap success ranged from 0 - 80 individuals, individual traps were considered to be the sampling unit. Comparisons of the relative abundance of pygmy perch in the floodplain and river were made using standard t-tests or Kruskal-Wallis Chi-square tests. Probability values were tested using the sequential Bonferonni technique (Holm 1979) to eliminate bias of a single test significance value (Rice 1989). Habitats within sites were compared using one-way ANOVAs or Kruskal-Wallace Chi-square tests. All among group pair-wise comparisons were undertaken in conjunction with the Tukey-Kramer HSD test for all comparisons. The alpha level was set at 5%.

RESULTS

The same fish species occurred at the three study sites over the sampling period, except that *N. australis* was absent from Woady Yaloak River (Table 1). Additional species collected were *Anguilla australis* (Short-finned eel), *Perca fluviatilis* (Redfin) and *Gambusia holbrooki* (Eastern mosquitofish).

Our results indicate different patterns of temporal and spatial variation in abundance of pygmy perch

Study Site	Sample	*Nannoperca australis*	*Nannoperca obscura*	*Anguilla australis*	*Perca fluviatilis*	*Gambusia holbrooki*
Deep Creek 1	Sept.	15	5	0	0	2
	Oct.	68	18	0	0	5
	Nov.	1100	25	1	1	4
	Dec.	1162	28	2	0	8
Deep Creek 2	Sept.	39	3	0	0	1
	Oct.	74	7	4	0	5
	Nov.	356	20	6	0	7
	Dec.	396	11	2	15	5
	Jan.	314	4	6	27	5
Woady Yaloak River	Dec.	0	135	1	1	2
	Jan.	0	267	1	2	3

Table 1. Total number of fish collected in funnel traps during monthly sampling events between spring 1998 and summer 1999.

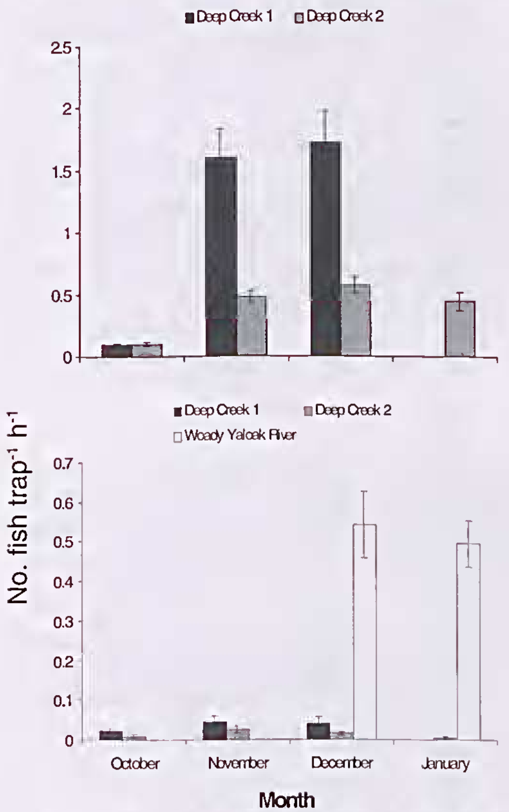

Fig. 1. Mean (± 1 SE) relative abundance (number of fish caught/trap/hour) during spring and summer of (i) *N. australis* at Deep Creek 1 and Deep Creek 2, and (ii) *N. obscura* at Deep Creek 1, Deep Creek 2 and Woady Yaloak River. Woady Yaloak River not sampled in October and November, and Deep Creek 1 was not sampled in January (see text).

populations (Fig. 1). While sizable increases in the relative abundance of *N. australis* occurred in November at both Deep Creek sites, the increase at Deep Creek 1 was substantially greater than at Deep Creek 2. In contrast, *N. obscura* showed little temporal variation at the Deep Creek sites. However, relative abundances of *N. obscura* at Woady Yaloak River were an order of magnitude larger than at both Deep Creek sites.

Length frequency data (Fig. 2) indicated that September samples of *N. australis* from both sites consisted of a small number of adults. Spawning *N. australis* females collected from Deep Creek 1 in September were significantly larger than those collected at Deep Creek 2 (Mean SL= 40.4mm vs. 32.9mm: Kruskal-Wallis Chisquare, X^2=10.31, d.f.=1, p=0.001). While substantial increases in its abundance occurred at both sites in November as a result of juvenile recruitment, the increase was much smaller at Deep Creek 2 despite similar aduult abundances two months earlier. Sample size was insufficient to compare size of *N. obscura* spawning females. The relatively small adult populations and low juvenile recruitment of *N. obscura* resulted in little change to abundances at both Deep Creek sites over the sampling period.

Significantly more *N. obscura* were trapped on the floodplain compared to the river at Woady Yaloak (Table 2). In contrast, larger numbers of *N. obscura* were trapped in the river at Deep Creek 1. Trapping success for *N. australis* at this site was significantly greater on the floodplain than in the river for all trapping episodes. These results indicate that *N. obscura* freely utilised the floodplain in allopatry but were seldom found there when sympatric with *N. australis*.

The patterns of habitat use by *N. australis* (Fig.

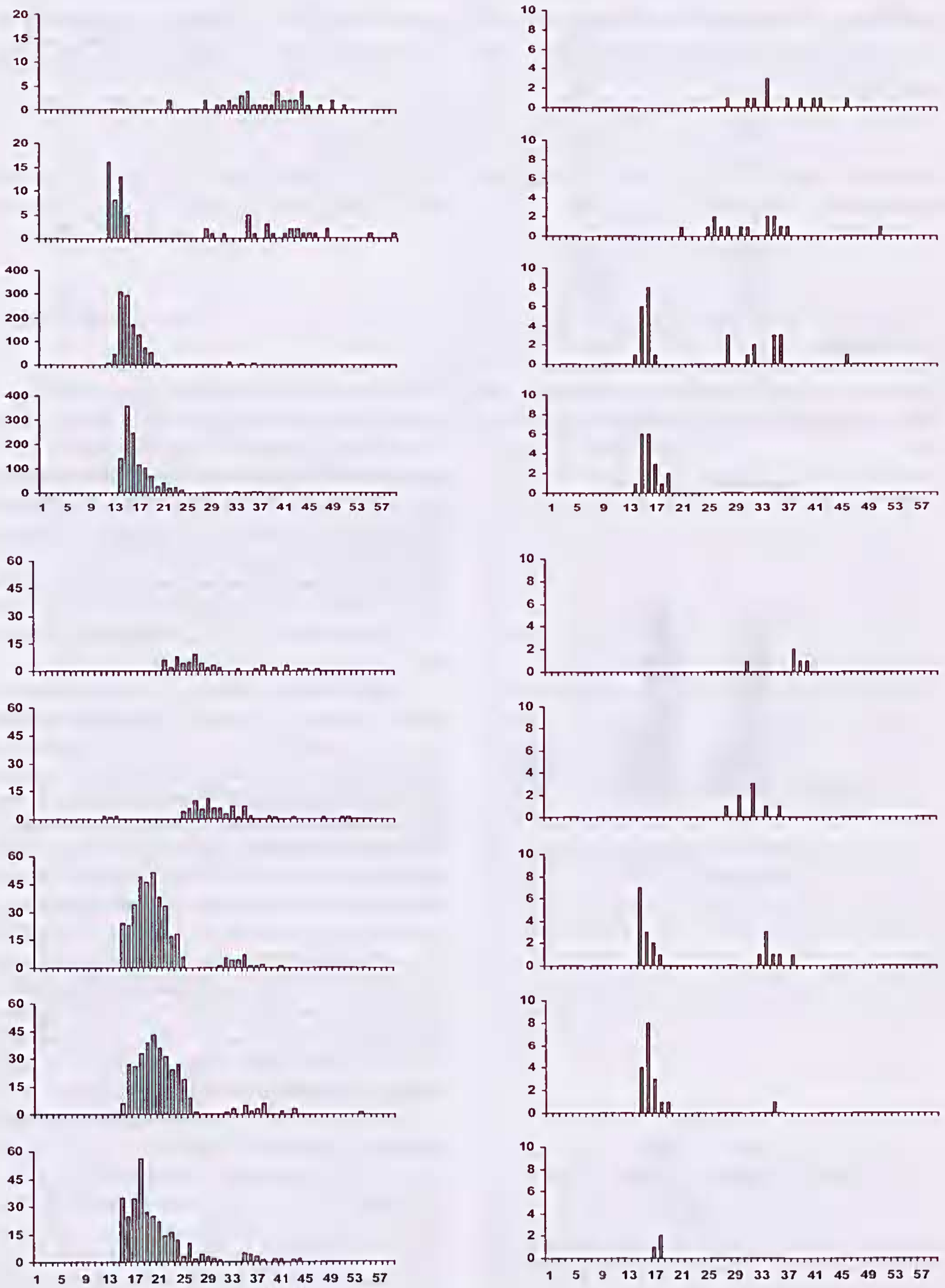

Fig. 2. Size variation (standard length in mm) of (i) *N. australis* and (ii) *N. obscura* individuals collected from (a) Deep Creek 1 and (b) Deep Creek 2 between September 1998 and January 1999. (Note the different scales on the Y-axis and that adult *N. australis* are not visible in November/December at Deep Creek 1 because of scale)

3) and *N. obscura* (Fig. 4) differed at both Deep Creek sites in that *N. australis* utilised all available habitats, but *N. obscura* was largely restricted to only two habitats (those with both submerged and emergent feathery plants and the channel). At Woady Yaloak River *N. obscura* used all available habitats (Fig. 5). While the types of habitats at the two streams were very similar, the pattern of habitat use by *N. obscura* differed when *N. australis* was present. *Nannoperca obscura* exhibited a similar pattern of habitat use to that of *N. australis* when in allopatry. All vegetated habitats were occupied, and relatively few individuals were trapped in the channel.

The number of potential predators of pygmy perch caught in each habitat is shown in Table 3. We recorded pygmy perch in stomach contents of a small number of *P. fluviatilis* and *A. australis* (unpublished data). While pygmy perch were not recorded from *G. holbrooki* in this study, it is likely to be a predator of only eggs and larvae. Relatively large numbers of *A. australis* and *P. fluviatilis* were collected at Deep Creek 2 compared to Deep Creek 1, suggesting that their abundance was greater at the former site. *Anguilla australis* was caught in all habitats except the channel. *Perca fluviatilis* was caught in all habitats, with the largest numbers occurring in channel habitats and those with submerged and emergent feathery vegetation. *Nannoperca obscura* was also largely restricted to these habitats at this site. Relatively small numbers of *P. fluviatilis* were caught at Woady Yaloak River.

DISCUSSION

Unbaited funnel traps proved to be an effective and non-intrusive way of capturing pygmy perch. Although variation in trapping success of pygmy perch may have been influenced by several factors, including fish density, fish activity, trapping effort and trap density, the sampling regime used in the study probably provided good estimates of the abundances of both species among sites and habitats. However, trapping success of funnel traps undoubtedly produced underestimates of predator abundances because of size bias.

The patterns of temporal changes in abundance of *N. obscura* and *N. australis* at the study sites may have been due to differences in fecundity, spawning success, mortality (particularly of juveniles) and/or emigration. Adult populations of *N. obscura* were much smaller than those of *N. australis* at Deep Creek, but juvenile recruitment was also substantially lower than expected based upon adult numbers in the spring, particularly at Deep Creek 2. Fecundity of a *N. australis* stream population was found to range from 78 to 679 (Humphries, 1995), depending upon female size. While the fecundity of *N. obscura* is not known, it may be similar to that of *N. australis* given the similar size and shape of the two species. Although *N. obscura* was not sampled from the Woady Yaloak River site in spring, samples collected in summer suggest that adult survivorship and juvenile recruitment was relatively high, resulting in summer populations that were an order of magnitude larger than the Deep Creek sites.

Abundance patterns of *N. australis* may have been largely determined by differences in fecundity and predator abundance at a site. The lower number of individuals at Deep Creek 2 may have been partly due to the smaller body size of spawning females. Fecundity in *N. australis* has been found to be correlated with body size (Humphries 1995). Intraspecific variation in fecundity is common in fish (Healy & Heard 1984; Humphries 1989) and may be due to factors such as variation in food supply (Bagenal 1969) and age/size dependent mortality (Reznick & Endler 1982).

The larger number of *P. fluviatilis* and *A. australis* caught at Deep Creek 2 also suggests that the lower numbers of *N. australis* at this site during spring-summer may have been due in part to larger populations of these predators of pygmy perch. While abundances of *N. obscura* among sites may have also been influenced by predation by these piscivores, competition with *N. australis* (see below) may have resulted in higher predation rates of *N. obscura* at Deep Creek (especially Deep Creek 2) compared to Woady Yaloak River.

The floodplain was utilised by both species of pygmy perch during late spring - early summer when available at Deep Creek and Woady Yaloak River. *Nannoperca australis* was found in significantly higher numbers on the floodplain compared to the main river at Deep Creek 1. *N. obscura* was also caught in significantly higher numbers on the floodplain at Woady Yaloak River however, it was virtually absent from this habitat at Deep Creek 1. While floodplain habitat does not appear to be essential for *N. australis* and *N. obscura*, the relative abundance of *N. obscura* was lower when absent from the floodplain (Deep Creek 1), or when a floodplain failed to develop because of channel characteristics (Deep Creek 2).

Floodplain habitat is important to many native fish, particularly as a nursery providing plentiful food (Geddes & Puckridge 1988). Floodplains also appear to be utilised by other species of pygmy perch as nurs-

Species	Site	Sample	Total Number of Fish (floodplain)	Relative abundance (floodplain)	Total Number of Fish (main river)	Relative abundance (main river)	t-test/X^2	d.f.	p value
N. australis	Deep Creek 1	Oct.	50	0.14 ±0.03	18	0.05±0.02	-2.99 [a]	70	0.004
		Nov.	766	2.25 ±0.39	334	0.95 ±0.23	-3.06 [a]	70	0.003
		Dec.	787	2.38 ±0.40	375	1.07 ±0.26	-2.79 [a]	70	0.007
N. obscura	Deep Creek 1	Oct.	0	0 ±0	18	0.48 ±0.02	11.37 [b]	1	<0.001
		Nov.	3	0.01 ±0.01	25	0.08 ±0.03	9.68 [b]	1	0.002
		Dec.	0	0 ±0	28	0.08 ±0.03	8.84 [b]	1	0.003
N. obscura	Woady Yaloak River	Dec.	104	0.84 ±0.11	30	0.24 ±0.06	-5.27 [a]	26	0.001

[a] =t-test [b] =X^2(Kruskal-Wallis Chisquare)

Table 2. Total number and comparison (t-test or Kruskal-Wallis Chisquare test) of the mean (±1 SE) relative abundance (number of fish caught/trap/hour) of *N. australis* and *N. obscura* on the floodplain and main river at Deep Creek 1 and Woady Yaloak River.

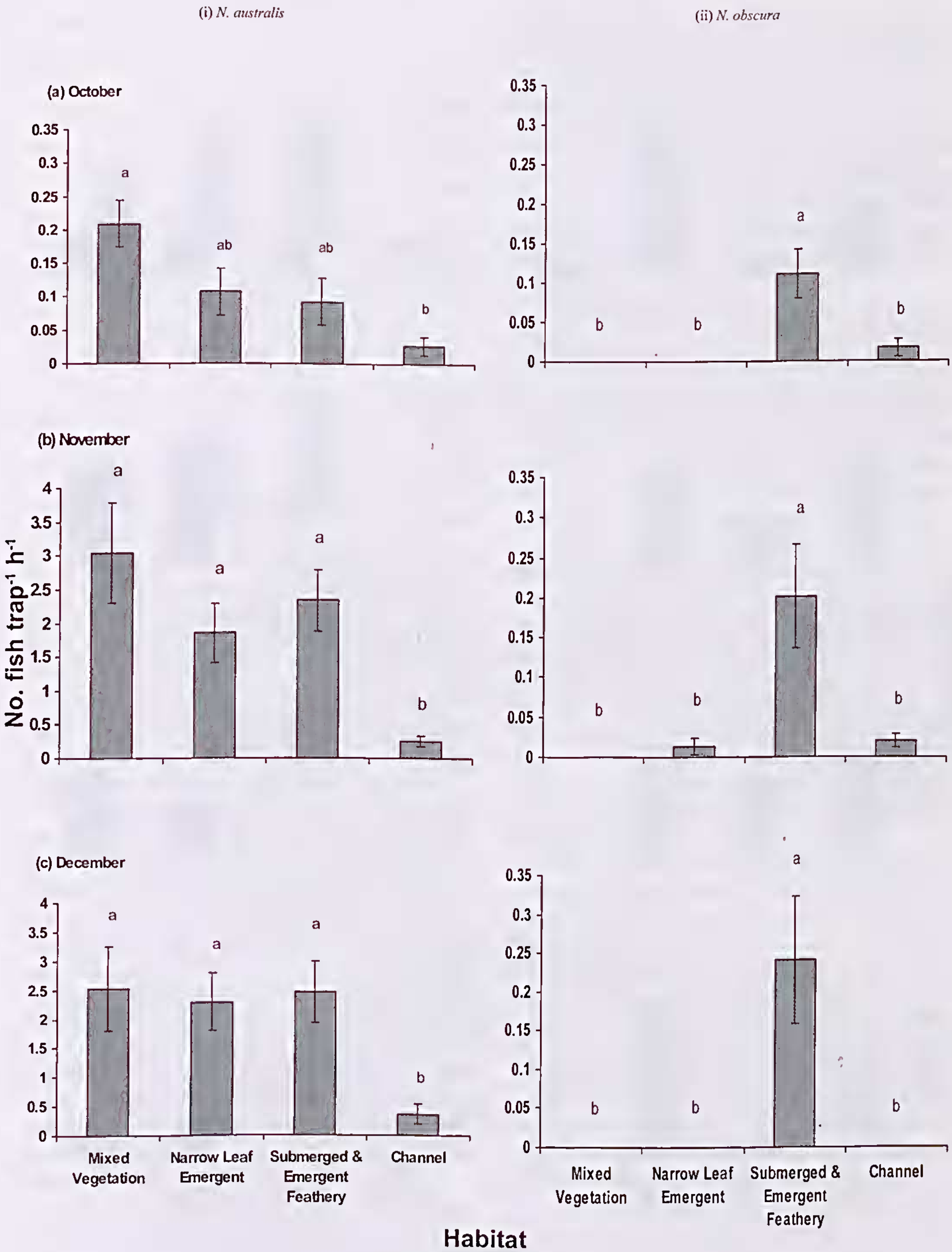

Fig. 3. Trapping success (number of fish caught/trap/hour) for *N. australis* and *N. obscura* at each habitat in Deep Creek 1. Tukey-Kramer tests were used to compare all habitat pairs. Means with the same letter are not significantly different ($p \geq 0.05$) for that graph. Note the different scales on the Y axes..

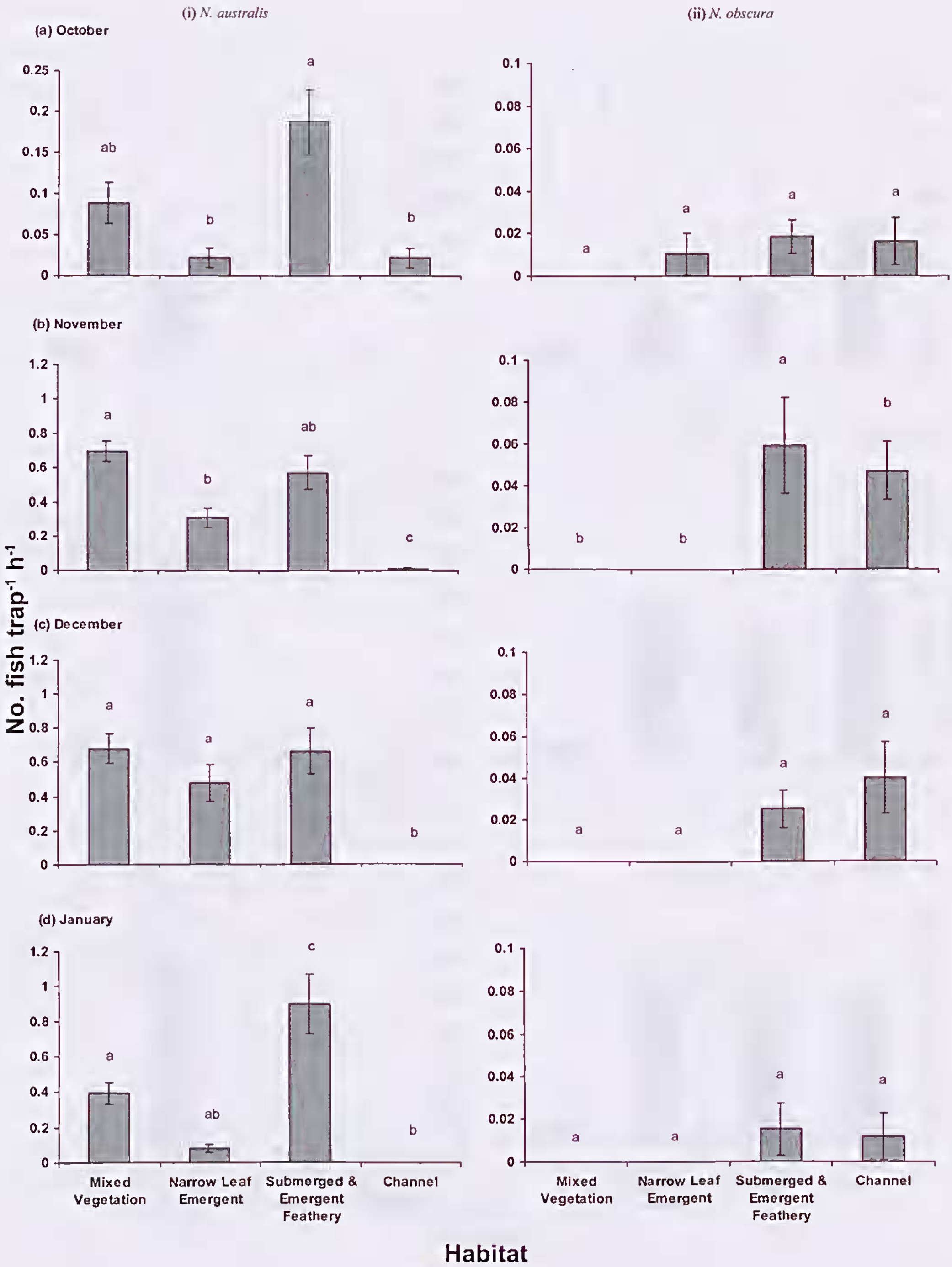

Fig. 4. Trapping success (number of fish caught/trap/hour) for (i) *N. australis* and (ii) *N. obscura* in each habitat at Deep Creek 2. Tukey-Kramer tests were used to compare all habitat pairs. Means with the same letter are not significantly different ($p \geq 0.05$). Note the different scales on the Y axes.

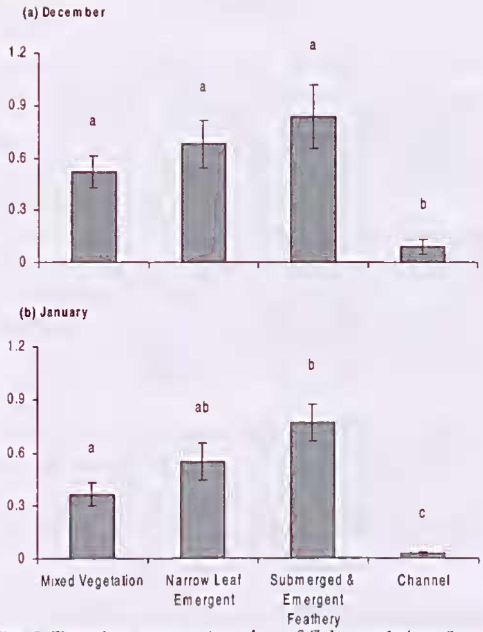

Fig. 5. Trapping success (number of fish caught/trap/hour) for *N. obscura* in each habitat at Woady Yaloak River. Tukey-Kramer tests were used to compare all habitat pairs. Means with the same letter are not significantly different ($p \geq 0.05$).

eries. *Nannatherina balstoni* (Balston's pygmy perch) (Morgan et al. 1995) and *Edelia vittata* (Western pygmy perch) (Pen & Potter 1991) move onto the floodplain after heavy flooding prior to spawning.

Nannoperca australis and *N. obscura* have been previously associated with aquatic macrophytes (Llewellyn 1974; Cadwallader 1979; Jackson & Davies 1983). This close association was also exhibited by both species in this study. While *N. australis* showed only an occasional preference for particular vegetated habitats, the channel habitat was generally avoided. Backhouse & Gooley (1979) and Humphries (1995) found *N. australis* has a strong preference for shallow water with low to zero velocity. The channel habitats at Deep Creek were characterised by deep water, little vegetation, and stronger current flows compared to other habitats, which probably accounts for the low number of *N. australis* recorded in this habitat.

While habitat floristics do not appear to be important, *N. australis* was trapped at relatively low numbers in areas containing *Myriophyllum*, despite the high density of macrophytes and shallow water. Relatively large numbers of *P. fluviatilis* were also caught in these areas, and some had been feeding on pygmy perch. Humphries (1995) indicated that *N. australis* is an important prey item for *P. fluviatilis*, and Hutchinson (1991) provided circumstantial evidence that *P. fluviatilis* was responsible for eliminating *E. vittata* (western pygmy perch) from many sites in the Murray River in Western Australia. While the relatively low numbers of *N. australis* trapped in this habitat may have been due to *P. fluviatilis* predation, fish are known to respond to predators by moving to habitats providing protection (Cerri & Fraser 1983; Werner et al. 1983).

While the pattern of habitat use by *N. obscura* was similar to that of *N. australis* in allopatry, it was essentially restricted to only one of the vegetated habitats and the channel habitat when sympatric. The habitat restriction of *N. obscura* at Deep Creek may be due to past or current interspecific competitive interactions (Connell 1980), habitat preferences of the species (Nilsson 1967; Wootton 1990) or predator avoidance (Cerri & Fraser 1983; Werner et al. 1983).

We speculate that the different patterns in abundance of pygmy perch among sites were largely due to interactions between size-fecundity relationships, habitat use sometimes mediated by interspecific competition, and predation intensity. Mortality rates due to predation will be influenced by predator abundance and encounter rates (Ware 1972). While abundances of *N. australis* may be influenced by overall predator abundances, predation rates on *N. obscura* may be higher when sympatric with *N. australis* because of its restriction to habitats with high predator abundances, in particular *P. fluviatilis*.

Observations of niche shifts and associated changes in mortality provide some of the best evidence that competition plays an important role in determining ecological assemblage and community characteristics. It appears that the competition for space between *N. australis* and *N. obscura* and predation by *P. fluviatilis* may influence habitat use and relative abundances of the two species. This suggests that the differential decline in *N. australis* and *N. obscura* populations since European settlement may be due to the competitive superiority of *N. australis* and habitat use by *N. obscura, N. australis* and *P. fluviatilis*. Stronger evidence that these biotic interactions underlie the differential decline of *N. obscura* and *N. australis* would require more replicate sites for each assemblage type, further sampling over time to establish assemblage stability, and/or removal experiments.

Site	Species	Mixed Vegetation	Narrow Leaf Emergent	Submerged & Emergent Feathery	Channel
Deep Creek 1	*Anguilla australis*	0.33	0.66	0.33	0
	Perca fluviatilis	0	0	0	0.33
	Gambusia holbrooki	1.33	1.0	2.33	0.66
Deep Creek 2	*Anguilla australis*	1.5	0.75	1.75	0
	Perca fluviatilis	1.0	1.0	4.75	3.75
	Gambusia holbrooki	1.75	1.75	1.75	1.0
Woady Yaloak	*Anguilla australis*	0.5	0	0.5	0
River	*Perca fluviatilis*	0	0	0.5	1.0
	Gambusia holbrooki	1.0	0	1.5	0

Table 3. Mean trapping success of pygmy perch predators (mean number of fish caught per trapping session) in different habitats at Deep Creek and Woady Yaloak River for all samples.

REFERENCES

Allen, G.R., Midgley, S.H. & Allen, M., 2002. *Field Guide to the freshwater fishes of Australia*. Western Australian Museum, Perth, 394 pp.

Backhouse, G. N. & Gooley, G. J., 1979. The fish fauna of Bridgewater lakes, Portland, Victoria. *Victorian Naturalist* 96, 232-238.

Bagenal, T. B., 1969. The relationship between food supply and fecundity in brown trout Salmo trutta. *Journal of Fish Biology* 1, 167-182.

Cadwallader, P. L., 1979. Distribution of native and introduced fish in the Seven Creeks River system, Victoria. *Australian Journal of Ecology* 4, 361-385.

Cerri, R. D. & Fraser, D. F., 1983. Predation and risk in foraging minnows: Balancing conflict demands. *American Naturalist* 121, 552-561.

Connell, J. H., 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35, 131-138.

DNRE, 1998. *Atlas of Victorian Wildlife*, Department of Natural Resources and Environment Victoria, Melbourne.

Geddes, M. C. & Puckridge, J. T., 1988. Survival and growth of larval and juvenile native fish: the importance of the floodplain. In *Proceedings of the Workshop on Native Fish Management*, M.C. Geddes, ed., Murray-Darling Basin Commission, Canberra, 101-115.

Groombridge, B. & Mace, G. (eds.). 1994. *1994 IUCN Red List of Threatened Animals*. International Union for conservation of Nature and Natural Resources, Gland, Switzerland.

Healy, M. C. & Heard, W. R., 1984. Inter- and intra-population variation in the fecundity of Chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. *Canadian Journal of Fisheries and Aquatic Sciences* 41, 476-483.

Holm, S., 1979. A simple sequential rejective multiple test procedure. *Scandinavian Journal of Statistics* 6(65), 65-70.

Humphries, P., 1989. Variation in life history of diadromous and landlocked populations of the spotted galaxias, *Galaxias truttacens* Valenciennes, in Tasmania. *Australian Journal of Marine and Freshwater Research* 40, 501-518.

Humphries, P., 1995. Life history, food and habitat of the Southern Pygmy Perch, *Nannoperca australis*, in the Macquarie River, *Tasmania. Marine and Freshwater Research* 46, 1156-1169.

Hutchinson, M. J., 1991. Distribution patterns of Redfin Perch *Perca fluviatilis* Linneus and Western Pygmy Perch *Edelia vittata* Castelnau in the Murray River System Western Australia. *Records of the Western Australian Museum* 15(1), 295-301

Jackson, P. D. & Davies, J. N., 1983. Survey of the fish fauna in the Grampians region, South-Western Victoria. *Proceedings of the Royal Society of Victoria* 95, 39-51.

Kesteven, G.L., 1960. Manual of field methods in fisheries biology. In *Manuals in Fisheries Sciences No. 1*, F.A.O., Rome, 152 pp.

Koehn, J. D. & O'Connor, W. G. 1990. *Biological information for management of native freshwater fish in Victoria*. Department of Conservation and Environment, Freshwater Fish Management Branch, Arthur Rylah Institute for Environmental Research, Melbourne, 165 pp.

Kuiter, R. H. & Allen, G. R., 1986. A synopsis of the Australian pygmy perches (Percichthyidae), with the description of a new species. *Revue française Aquariologie* 12, 109-116.

Kuiter, R. H., Humphries, P. A. & Arthington, A. H., 1996. Family Nannopercidae. In *Freshwater Fishes of South-Eastern Australia*, 2nd edn, R. M. McDowell, ed., Reed, Sydney, 168-175.

Llewellyn, L. C., 1974. Spawning, development and distribution of the southern pygmy perch *Nannoperca australis australis* Gunther from inland waters in eastern Australia. *Australian Journal of Marine Freshwater Research* 25, 121-149.

Morgan, D. L., Gill, H. S. & Potter, I. S. 1995. Life cycle, growth and diet of Balston's pygmy perch in its natural habitat of acidic pools in south-western Australia. *Journal of Fish Biology* 47, 808-825.

Nilsson, N., 1967. Interactive segregation between fish species. In *Biological basis of freshwater fish production*, S. D. Gerking ed., Blackwell Scientific Publication, Oxford, U.K., 295-300.

Pen, L. J. & Potter, I. C., 1991. Biology of the Western pygmy perch, *Edelia vittata*, and comparisons with two other teleost species endemic to south-western Australia. *Environmental Biology of Fishes* 31, 365-380.

Reznick, D. & Endler, J. A., 1982. The impact of predation in life history evolution in Trinidadian guppies: genetic basis of observed life history patterns. *Evolution* 36, 160-177.

Rice, W. R., 1989. Analysing tables of statistical tests. *Evolution* 43(1), 223-25.

SAS Institute Inc., 1995. *JMP Statistics and Graph-*

ics Guide version 3.01. Cary, North Carolina, U.S.A.

SCHAEFFER, R. L., MENDENHALL, W. & OTT, R., 1996. *Elementary Survey Sampling*. Duxbury Press, Washington, 125-195.

SOKAL, R. R. & ROHLF, F. J., 1995. *Biometry*. W. H. Freeman and Company, New York.

SUTHERLAND, W. J., 1996. *Ecological Census Techniques*. Cambridge University Press, Cambridge, 336 pp.

WAGER, R. & JACKSON, P. D., 1993. *The Action Plan for Australian Freshwater Fishes*. Australian Nature Conservation Agency, Endangered Species Program No.147. Canberra.

WARE, D. M., 1972. Predation by rainbow trout (Salmo gairdneri): The influence of hunger, prey density and prey size. *Journal of the Fisheries Research Board of Canada* 29, 1193-1201

WERNER, E. E., GILLIAM, J. F., HALL, D. J. & MITTELBACH, G. G., 1983. An experiment test of the effects of predation risk on habitat use in fish. *Ecology* 64, 1540-1548.

WOOTTON, R. J., 1990. Introduction: tactics and strategies in fish reproduction. In *Fish Reproduction: Strategies and Tactics*. G. W. Potts & R. J. Wootton eds, Academic Press, London, 1-12.

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